# Pain experience in hermit crabs?

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## ARTICLE INFO

Pain may be inferred when the responses to a noxious stimulus are not reflexive but are traded off against other motivational requirements, the experience is remembered and the situation is avoided in the future. To investigate whether decapods feel pain we gave hermit crabs, *Pagurus bernhardus*, small electric shocks within their shells. Only crabs given shocks evacuated their shells indicating the aversive nature of the stimulus, but fewer crabs evacuated from a preferred species of shell indicating a motivational trade-off. Some crabs that evacuated attacked the shell in the manner seen in a shell fight. Most crabs, however, did not evacuate at the stimulus level we used, but when these were subsequently offered a new shell, shocked crabs were more likely to approach and enter the new shell. Furthermore, they approached that shell more quickly, investigated it for a shorter time and used fewer cheliped probes within the aperture prior to moving in. Thus the experience of the shock altered future behaviour in a manner consistent with a marked shift in motivation to get a new shell to replace the one occupied. The results are consistent with the idea of pain in these animals.
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Nociception is the ability to detect a noxious, potentially tissue-damaging, stimulus and respond to it (Sneddon 2004) whereas pain is the associated unpleasant, emotional interpretation or feeling associated with that perception (Broom 2007). There can be little doubt that decapod crustaceans have a nociceptive ability as they readily detect and withdraw from noxious stimuli (Kawai et al. 2004; Barr et al. 2008). However, there is a debate whether they are able to experience the emotional component (Sherwin 2001; Broom 2007; Barr et al. 2008), driven, in part, by a concern for the implications for the welfare of these animals, which are widely used in fishing, aquaculture and the general food industry. Since animals cannot be asked directly, indirect methods and argument by analogy may be applied in an attempt to answer this question (Sherwin 2001). Thus a species is considered to have the potential to feel pain if it fulfils certain criteria, such as: having a suitable nervous system; displaying protective motor reactions; showing trade-offs between stimulus avoidance and other motivational requirements; having opioid receptors; reduction of responses to noxious stimuli by analgesics and local anaesthetics; having high cognitive abilities; showing avoidance learning (Elwood et al., in press). We briefly consider these points with respect to decapods.

The neocortex has a central role in human pain and it has been argued that any species lacking this structure will be incapable of that feeling (Rose 2002). However, it is possible that different structures may be involved in the pain experience of other animals, in the way that decapods have vision despite lacking a human visual cortex (Elwood et al., in press). Thus it is difficult to determine whether or not decapods have a suitable nervous system and we must look more to behaviour to test whether they feel pain. Prawns, *Palaemon elegans*, show protective motor reactions when their antennae are treated with a noxious substance (Barr et al. 2008). They specifically groom the treated antennae and rub them against the tank, showing the animals are aware of the location of the noxious stimulus. Motivational trade-offs occur in crabs, *Carcinus maenas*, that receive a shock in a dark shelter in that they are more likely to leave the shelter after the shock if the ambient light is low, indicating an interaction of motivational systems (S. Barr, F. Mansoor & R. W. Elwood, unpublished data). Opioid receptors are present in decapods (Dyakonova 2001) and morphine inhibits the defensive response to an electric shock in the crab *Chasmagnathus granulatus* in a dose-dependent manner (Lozada et al. 1988).

The cognitive abilities of hermit crabs in information gathering and decision making are impressive. They rely on the use of gastropod shells for shelter and shells of adequate size, shape and strength, but without being too heavy (Briffa & Elwood 2005), are a key resource (Elwood & Neil 1992). A hermit crab gathers information about shells by vision (Reese 1963) but this information is enhanced during approach and contact. After contact it grasps the shell with its walking legs and chelipeds and explores the exterior, moving its chelipeds over the surface, and then turns the shell so

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that the aperture is uppermost and begins to investigate the interior by inserting one or both chelipeds or sometimes a walking leg. It obtains detailed information as to the size, internal volume, shell species (shape) and weight during this process and assesses the overall quality relative to that of the shell it is currently occupying (Elwood & Stewart 1985; Jackson & Elwood 1989a; Elwood 1995). The crab may move into the new shell and test the inside of the shell by thrusting the abdomen back and forth. It might also investigate the interior and exterior of the original shell and even move back into it, assessing which is the better of the two (Elwood 1995). Hence these crabs demonstrate sophisticated shell investigation behaviour, remembering the information gathered at each stage of the investigation, and also remembering specific shells for up to 40 min (Jackson & Elwood 1989b). They may also fight another crab over ownership of shells in which case information about the shells and the opponent is integrated with information about their own physiological state (Briffa & Elwood 2004). They can remember previous opponents for up to 4 days (Gherardi & Atema 2005) and it has been suggested that they may select which crabs to fight on the basis of their perception of how their current shell might suit the opponent (Hazlett 1996). Thus crabs have the ability to gather and use information from a variety of sources and to make comparisons between shells and between opponents.

The main function of the unpleasant feeling of pain is that the animal will remember the circumstances that led to it and avoid those in the future (Bateson 1991; Broom 2001). Avoidance learning has been demonstrated in crayfish, *Procambarus clarkii* (Kawai et al. 2004), which escape into another compartment of the tank to avoid an electric shock. Additionally, connections from nociceptors to learning centres are found in decapods (Sandeman et al. 1992). Thus decapods show features that are consistent with the idea of pain.

Preliminary tests have shown that electric shock delivered to the abdomen within the shell causes hermit crabs to evacuate their shells when sufficiently severe. The object in the present study was to give some crabs shocks at just below the threshold required for the majority of crabs to evacuate whereas others were not shocked. We determined whether the quality of shell influenced the decision to evacuate and thus whether there was a trade-off between conflicting motivational demands. Crabs that retained the shell were subsequently offered a new shell and we determined whether the quality of the existing shell and the prior experience of shock influenced their subsequent responses towards that shell. Immediate evacuation of a shell when shocked may be viewed as a simple, nociceptive reflex but here we examined whether a noxious stimulus that is not strong enough to cause this is nevertheless remembered and used in subsequent decision making about changing shells. Thus we investigated how the motivation of the animal is altered by a previous noxious stimulus. A significant effect would demonstrate a memory of the experience, an awareness of the location of the noxious stimulus and the use of actions that are appropriate to escape from the situation after the stimulation has ceased. We thus investigated nonreflexive responses that might be consistent with the concept of pain in these crustaceans.

## METHODS

Hermit crabs, *Pagurus bernhardus*, were collected from rock pools at the shore at Ballywalter, Co Down, Northern Ireland, U.K. (54°32′0″N, 5°29′0″W) in May and June 2008 at low tide. They were transported to Queen's University, Belfast, and housed in aerated sea water tanks (changed every 3 days), maintained between 11 and 13 °C on a 12:12 h light:dark cycle. They were cracked out of their shells using a bench vice before the day of testing and given either an experimental *Littorina obtusata* or

*Gibbula cineraria* shell. The former species is much preferred to the latter as shown by choice experiments (Elwood et al. 1979) and escalation of shell fights (Dowds & Elwood 1983). Testing occurred between 0800 and 1400 hours the following day. The hermit crabs were transferred into nonexperimental shells afterwards and brought back to the same shore and released.

The experimental shells were modified so we could deliver shocks while the hermit crab was inside the shell. Two small holes (diameter 1 mm) were drilled into the experimental shells. We scraped off the resin at each end of two resin-insulated copper wires (diameter 0.23 mm), put each of them through the holes in the shell, fixed the wires with resin and bent them flush with the interior wall of the shell. A range of shells was used to cover the size range of crabs found on the shore and each experimental shell was the optimum weight for that shell species for the size of crab (Jackson & Elwood 1989a).

Hermit crabs were randomly assigned to a shock or no-shock group. They were placed individually in a sea water-filled plastic pot (diameter: 12 cm; height: 10 cm) and wires were connected to the stimulator and fixed above the pot so that the crabs could walk at any point in the pot. The shock group received a shock of 8 V with a duration of 1 s and a frequency of 200 Hz (a level lower than normally required to effect immediate evacuation), delivered every 20 s until 10 shocks had been applied ($N = 55$; 33 in *L. obtusata*, 22 in *G. cineraria*). In the no-shock group nothing happened for 240 s ($N = 49$; 27 in *L. obtusata*, 22 in *G. cineraria*). Twenty seconds after the last shock (or after the 240 s in the no-shock group) another shell of the same weight and species as the experimental shell, but without electrodes, was offered and put ca. 5 cm away from the crab with the aperture downwards. This disturbance typically caused the crabs to withdraw temporarily into their shells.

We recorded the time of approach (time from re-emergence from the shell to contact with the new shell) and of investigation of the shell (duration of touching outside and inside of the shell prior to moving in). Additionally, the number of times the crab puts its chelipeds into the shell during investigation were counted (cheliprobes). We also noted whether investigation led immediately to moving into the new shell or whether the crab moved away and then approached to resume investigation.

### Statistical Analyses

Categorical data on the numbers of animals performing particular actions were tested with Fisher's exact probability tests. Preliminary analysis of continuous data with ANOVA and ANCOVA showed no effect of gender, crab and shell weight on the dependent variables. A number of measured activities were not normally distributed and hence were log $(x + 1)$ transformed as necessary. MANOVA was used to compare crabs differing in shell species and treatment group (shock, no-shock) and then univariate ANOVA to examine significant components of the MANOVA.

### Ethical Note

No licence was required for this work within the United Kingdom as *Octopus vulgaris* is the only invertebrate covered by the Animals (Scientific Procedures) Act. Cracking the shell in a vice simply fractures the gastropod shell and the crab is not injured and quickly abandons the remnants of the shell. Once the crab was in experimental shell, we applied small electric shocks that were intended to be below the level that would cause the crab to leave the shell and thus not judged to be severe. If the crab abandoned the shell it removed itself from further shock. All animals seemed to recover from the experience and all were provided with suitable shells and returned to the shore.

## RESULTS

Significantly more crabs that were shocked evacuated the shell compared to those that were not shocked (Fisher's exact test: shock: 14/55; no-shock: 0/49; $P = 0.0005$). Shocked crabs were less likely to evacuate from the preferred species (4/33 *L. obtusata* and 8/22 *G. cineraria*; Fisher's exact test: $P = 0.047$). There was no effect of shell species on whether they moved back to the shell (0/4 *L. obtusata* and 5/8 *G. cineraria*; Fisher's exact test: NS); those that did were included in the analysis given below. However, a further eight withdrew deep into the shell during shock (6 in *L. obtusata* and 2 in *G. cineraria*; Fisher's exact test: NS) and remained thus for 15 min; these were not offered a new shell and are excluded from the analysis given below. In total, 89 crabs (*L. obtusata*: shock: 23; no-shock: 25; *G. cineraria*: shock: 17; no-shock: 24) were offered a new shell. Crabs that were shocked were more likely to approach (Fisher's exact test: shock: 34/40; no-shock: 31/49; $P = 0.030$) and take the offered shell than were those that were not shocked (Fisher's exact test: shock: 33/40; no-shock: 27/49; $P = 0.007$) but shell species did not influence approach or entry into the new shell of either shocked or nonshocked crabs. One shocked crab that evacuated each shell species showed rapping of the naked abdomen against the shell and one crab was observed to groom its abdomen. Of the 60 crabs that moved into the new shell, 56 did so after a single approach and investigation, and the analysis of times taken in the various activities given below excludes the four that approached and investigated more than once.

Of those 56 crabs, there was an overall effect of shock on the three continuous measures of behaviour (Wilk's $\lambda = 0.438$, $F_{3,50} = 21.398$, $P < 0.0001$) but no overall effect of shell species (Wilk's $\lambda = 0.886$, $F_{3,50} = 2.151$, $P = 0.106$) and no interaction effect (Wilk's $\lambda = 0.96$, $F_{3,50} = 0.688$, $P = 0.564$). Subsequent ANOVA showed that the shock group approached more quickly ($F_{1,52} = 24.59$, $P < 0.0001$; Fig. 1a), spent less time investigating the new shell prior to moving in ($F_{1,52} = 11.447$, $P = 0.001$, Fig. 1b) and used fewer cheliprobes ($F_{1,52} = 41.448$, $P < 0.0001$; Fig. 1c) compared to those not shocked.

## DISCUSSION

Hermit crabs rely on shells for their survival (Elwood & Neil 1992) and it is no surprise that those not receiving a shock did not evacuate their shells; however, some of those that received a shock did evacuate. The abandonment of this critical resource clearly demonstrates the aversive nature of the shock. Evacuation in this context might be viewed as a simple reflex response and thus demonstrate nociception rather than pain. However, crabs were more likely to evacuate from the less preferred species of shell, demonstrating a trade-off between competing motivational requirements, similar to that shown for fish (Millsopp & Laming 2008) and humans (Salomons et al. 2004). The two shell species have been shown to influence motivation differentially in a variety of contexts (Jackson & Elwood 1990; Elwood et al. 1998) but here they modulated the response to a noxious stimulus and this presumably involves a higher level of neural processing than seen in reflexive actions. We have also shown in our laboratory that hermit crabs evacuate at a lower voltage from less preferred shells (Appel & Elwood, in press) and that shore crabs are more likely to emerge from a dark shelter after shock if the ambient light is low (unpublished data). These observations of trade-offs are consistent with a pain experience.

Furthermore, of the relatively few crabs that evacuated after shock, grooming of the abdomen was seen in one and rapping of the abdomen against the empty shell in two. Grooming is a protective motor reaction and viewed as a sign of pain in
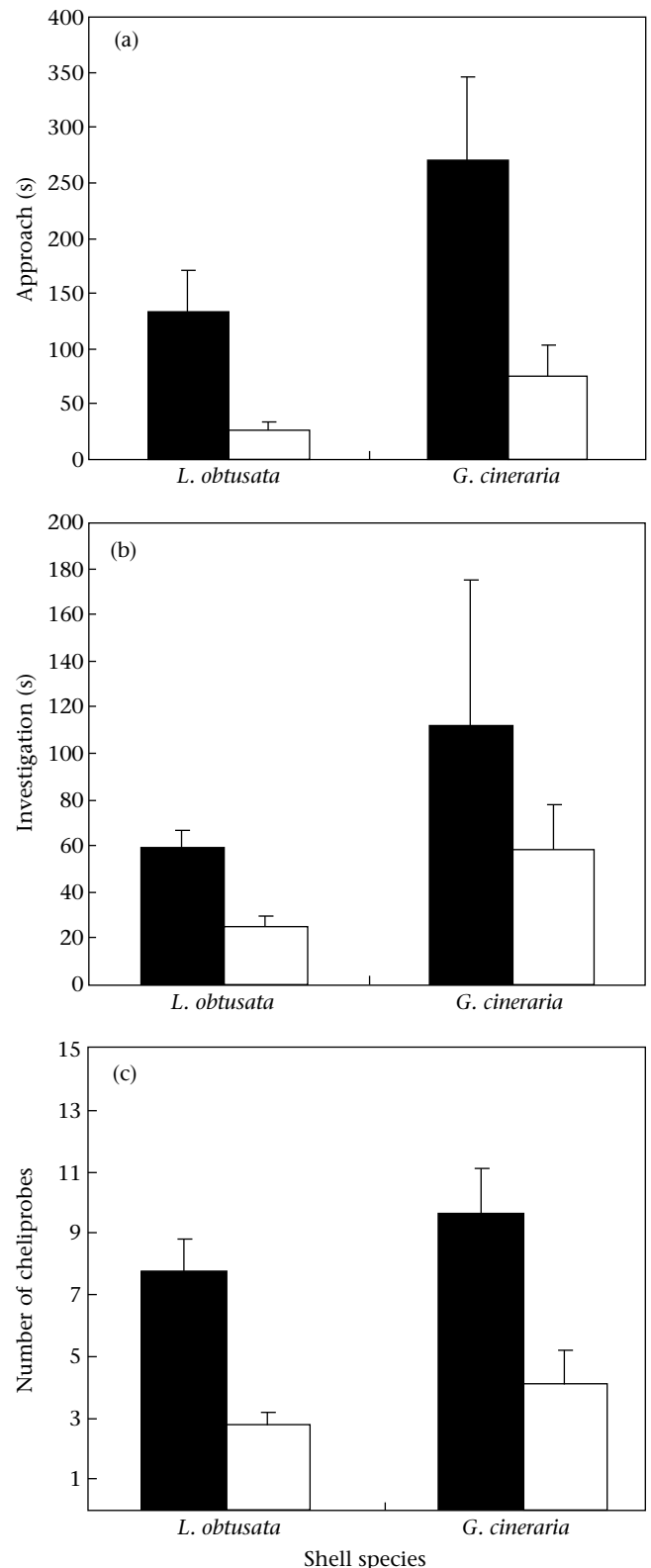


**Figure 1.** Mean ± SE of (a) time taken to approach (s), (b) duration of investigation (s) and (c) number of cheliprobes by crabs in either *L. obtusata* or *G. cineraria* shells that had been shocked (□) or not shocked (■).

vertebrates (Weary et al. 2006). It supports the idea of crabs being aware of the location of a noxious stimulus (Barr et al. 2008). Rapping the abdomen, while it is still in a shell, against a shell of another crab is a normal behaviour seen in fights over shells and

rapping with the naked abdomen has been observed in experimentally induced naked crabs against the shell occupied by another crab (Elwood & Glass 1981). Here it was observed against an unoccupied shell in which the crab had experienced a noxious event and there are similarities with shock-induced aggression in rats, *Rattus norvegicus* (Hutzell & Knutson 1972). Again these observations are consistent with the concept of pain.

The experience of the shock markedly influenced the subsequent behaviour in a manner consistent with the crabs now perceiving their shell as being of very low quality (Elwood & Stewart 1985; Elwood 1995). Significantly more shocked crabs approached and moved into the new shell compared to those not shocked. Furthermore, shocked crabs moved towards the new shells more quickly, spent less time investigating those new shells and used fewer probes of their chelipeds into the new shell prior to moving into the shell compared to those not shocked. That is, the shock influenced not only what they did but also the speed with which it was achieved and shows that the motivation to obtain a new shell had been markedly increased (Jackson & Elwood 1989a; Elwood 1995). Furthermore, the stimulation had ceased prior to the new shell being offered and the findings are difficult to interpret as a nociceptive reflex because the responses were delayed until an opportunity to express them was presented. At that time a complex sequence of activities enabled the crabs to move towards the shell, grasp it, assess it quickly as offering an improvement, release their abdominal hold on their existing shell and swing it into the new one. The data are consistent with the concept of memory of a painful event. The species of shell, however, did not significantly affect subsequent behaviour when the crabs were presented with a new shell. The new shells were of the same species as that occupied and thus there was no difference between the groups in terms of gain in shell quality. Previous experiments have indicated that crabs respond to potential new shells more positively if a large gain can be achieved and tend to move into shells offering a large gain more quickly than those offering a moderate gain (Elwood & Stewart 1985; Elwood 1995).

The ability to feel pain has been subject to natural selection and offers an advantage to those with this ability and thus pain may be taxonomically widespread (Bateson 1991; Broom 2001). There is increasing evidence that animals, other than mammals, experience pain (Sneddon 2004). Studies on birds (Gentle et al. 1991), amphibians (Stevens 1992; Machin 1999) and fish (Sneddon 2003; Sneddon et al. 2003; Dunlop et al. 2006; Millsopp & Laming 2008) all provide evidence consistent with pain. Such consistent evidence is frequently accepted as indicating pain because the behavioural responses shown to noxious stimuli are similar to those seen in mammals, including humans (Bateson 1991; Broom 2001). Because of that evidence, measures have been put in place in many jurisdictions for the protection of vertebrates in farming and research. However, similar evidence in invertebrates is often dismissed as not indicating pain (Sherwin 2001), possibly because invertebrates are perceived as having a lower value than vertebrates (Kellert 1993). We suggest that this stance should be re-evaluated and that there should be increased research on a diversity of animals with respect to their experience of noxious events.

## Acknowledgments

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